

# NUDIBRANCH DORIDS FROM THE PACIFIC COAST OF COSTA RICA WITH THE DESCRIPTION OF A NEW SPECIES

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## ABSTRACT

We describe a new species of opisthobranch dorid, *Atagema notacristata* sp. nov., from Costa Rica and Panama, and redescribe four species of dorids from the Pacific Coast of Costa Rica. *Atagema notacristata* is distinctive among the described taxa in having a unique combination of the following features: light brown background color with no conspicuous spots, compound tubercles with caryophyllidia uniformly arranged on the dorsum, short rhinophore sheaths, conical oral tentacles, five tripinnate branchial leaves, three branchial lobes, and a lobate blood gland. We redescribe *Geitodoris mavis* (Marcus and Marcus, 1967), *Doris immonda* (Risbec, 1928), *Doris pickensi* Marcus and Marcus, 1967, and *Doris tanya* Marcus, 1971, based on new material recently collected from the Pacific Coast of Costa Rica. *Doris immonda* represents the first record of this Indo-Pacific species in the Eastern Pacific.

The opisthobranch fauna of the Pacific Coast of Costa Rica has recently been reviewed (Camacho-García et al., 2005). More than 130 species have been reported from the region, including seven new records (Camacho-García, in press). Among nudibranch dorids, Camacho-García and Valdés (2003) reviewed the caryophyllidia-bearing dorids from Costa Rica and Fahey and Gosliner (2003) described a new species of *Hoplodoris* from the Pacific Coast of Costa Rica.

Here, we describe a new species of dorid and redescribe four other dorid species that were previously poorly described. We have added new anatomical data and compared their anatomy with similar congeners. We also discuss their distinguishing features and extend their known ranges into Costa Rican waters.

## METHODS

The material examined was hand-picked in the intertidal area or collected during snorkeling or SCUBA-diving. Some of the material was first stored at the Instituto Nacional de Biodiversidad (INBio), but is currently deposited at the Museo de Zoología of the Universidad de Costa Rica (MZUCR). Other material was obtained from the California Academy of Sciences (CAS).

The specimens were relaxed in magnesium chloride and preserved in a solution on Bouin's fixative. They were transferred to 70% ethanol after a week. The specimens were dissected by making a dorsal incision in the middle of the dorsum. The internal anatomy was examined and drawn under a dissecting microscope with a camera lucida (Nikon P6-5KE). At least two specimens of each species were dissected. The buccal mass was removed and placed in 10% sodium hydroxide until the jaws and radula were isolated from the tissue. The radula and jaws were rinsed in deionized water, and dried and mounted for examination with a scanning electron microscope (LEO 1450VP). Mantle samples were also taken, placed in 100% ethyl alcohol and critical-point dried. Photographs of living animals for most of the specimens were taken by the collectors. Notes and drawings on the external features of the living animals were also taken in the field by using a dissecting microscope (Nikon SMZ-1). Type material was not examined for the present study.

## SYSTEMATICS

## NUDIBRANCHIA Cuvier, 1817

## Family DISCODORIDIDAE Bergh, 1891

Genus *Atagema* J. E. Gray, 1850

*Type species: Doris carinata* Quoy and Gaimard, 1832 [= *Atagema carinata* (Quoy and Gaimard, 1832)], by monotypy.

*Atagema notacristata* new species

(Figs. 1A, 2A–F, 3A–D)

*Type Material*.—Holotype: Punta Uvita, Parque Nacional Marino Ballena, Area de Conservación Osa, Costa Rica (9°08'50"N, 83°46'16"W), 6 January 2002, 1 specimen (not dissected), 29 mm preserved length, intertidal, leg. Y. Camacho (MZUCR-INB0003701266).

Paratypes: West side of Isla Santa Catalina, Guanacaste, Costa Rica (10°28'57"N, 85°52'31"W), 17 April 2004, 1 specimen (not dissected), 21 mm preserved length, 13 m depth, leg. T. Gosliner (MZUCR-INB0003836160); Punta Ursula, Isla Jicarita, Panama (7°14'N, 81°48'W), 17 April 1993, 1 specimen (dissected), 11 mm preserved length, 9 m depth, leg. T. Gosliner (CASIZ 088219).

*Comparative Material Examined*.—Islas Murciélagos, Area de Conservación Guanacaste, Costa Rica (10°51'N, 85°53'W), 30 June 2005, 1 specimen, 14 mm preserved length, 5–13 m depth, leg. A. Hermosillo (MZUCR6997); Isla Catalina, Guanacaste, Costa Rica (10°28'47"N, 85°52'17"W), 16 January 2001, 2 specimens (dissected), 13–14 mm preserved length, 14–18 m depth, leg. S. Avila (MZUCR-INB0003118068); NE side of Punta Roble, Playa Real, Guanacaste, Costa Rica (10°23'12"N, 85°50'44"W), 20 April 2004, 1 specimen, 25 mm preserved length, 5 m depth, leg. T. Gosliner (MZUCR-INB0003836262); Parque Nacional Manuel Antonio, Costa Rica (9°23'02"N, 84°10'05"W), 19 February 2003, 1 specimen (dissected), 17 mm preserved length, 8–11 m depth, leg. A. Berrocal (MZUCR-INB0003572319); Isla Ballena, Parque Nacional Marino Ballena, Area de Conservación Osa, Costa Rica (9°06'18"N, 83°43'42"W), 18 January, 2003, 1 specimen (dissected), 14 mm preserved length, 18 m depth, leg. S. Avila (MZUCR-INB0003572307); Isla del Caño, Area de Conservación Osa, Costa Rica (8°43'01"N, 83°52'42"W), 13 January 2003, 1 specimen, 15 mm preserved length, 5–10 m depth, leg. S. Avila (MZUCR-INB0003572297).

*Etymology*.—This species is named *notacristata* because of the conspicuous crested ridge that is situated mid-dorsally on the notum.

*Distribution*.—This species is known from Bahía Banderas, Mexico (Hermosillo et al., 2006), Costa Rica (Camacho-García et al., 2005), and Coiba Island, Panama (present study).

*External Morphology*.—The body is oval and elongate (Fig. 1A). The dorsum has a very coarse texture due to the presence of many homogeneously arranged tubercles composed of numerous caryophyllidia. There is a very pronounced mid-dorsal ridge composed of fused tubercles; these tubercles are large and irregular, each having smaller tubercles on their apices and a very long cylindrical base surrounded by sev-

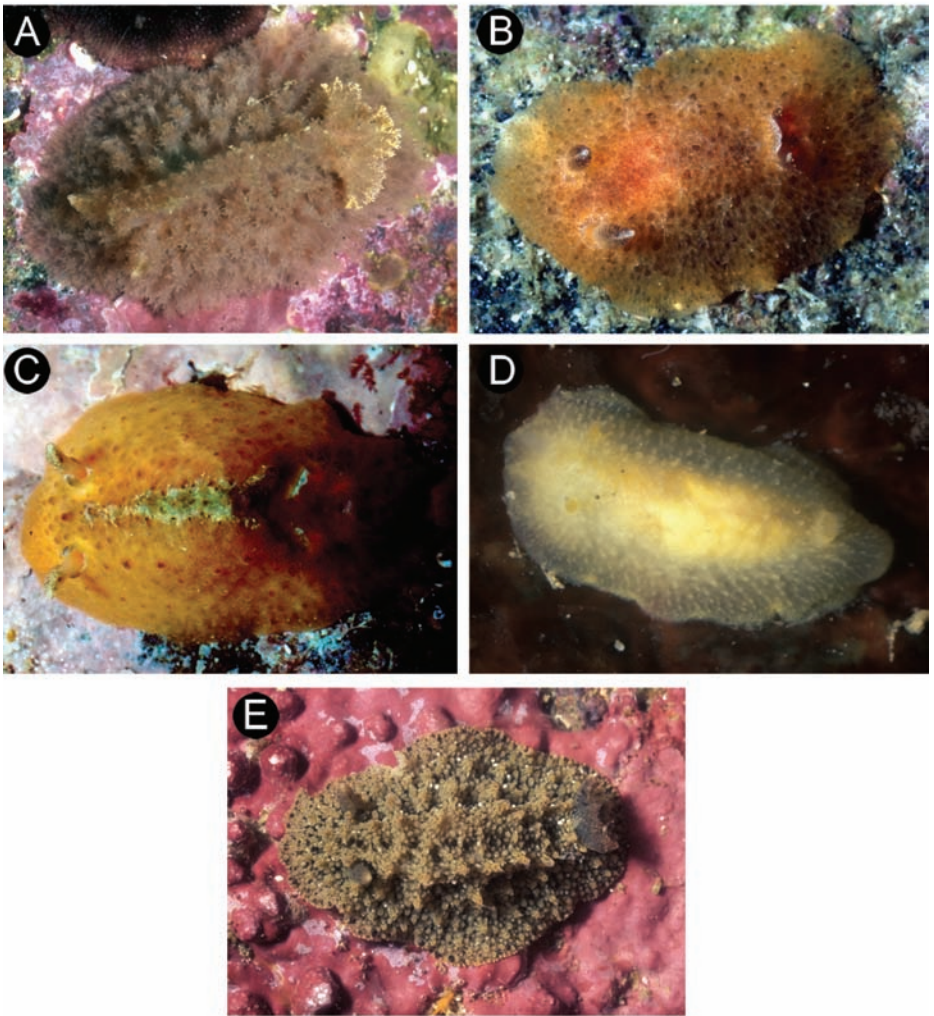


Figure 1. Photographs of live specimens. (A) *Atagama notacristata* sp. nov., Costa Rica (MZUCR-INB0003836262), Photo by T. Gosliner; (B) *Geitodoris mavis*, Costa Rica (MZUCR-INB0003836290), Photo by T. Gosliner; (C) *Doris immonda*, Costa Rica (MZUCR-INB0003836289), Photo by T. Gosliner; (D) *Doris pickensi*, Costa Rica (MZUCR-INB0001496424), Photo by T. Gosliner; (E) *Doris tanya*, Costa Rica (MZUCR-INB0003836280), Photo by T. Gosliner.

eral minute patches of cilia (Fig. 2A). The smaller apical tubercles are round, ciliated, and have small spicules around them. The rhinophoral sheaths are highly elevated and completely covered in tubercles and caryophyllidia. The branchial sheath is composed of three large lobes, with the middle one being the largest. There are five tripinnate branchial leaves. The anal papilla is elongate. The rhinophores are long, having 18 lamellae in a 25 mm preserved length specimen (MZUCR-INBI03836262) and 15 lamellae in a 17 mm, preserved length specimen (MZUCR-INBI03572319). Ventrally, the anterior border of the foot is notched and grooved. The oral tentacles are conical, and slightly wider at the base (Fig. 3A).

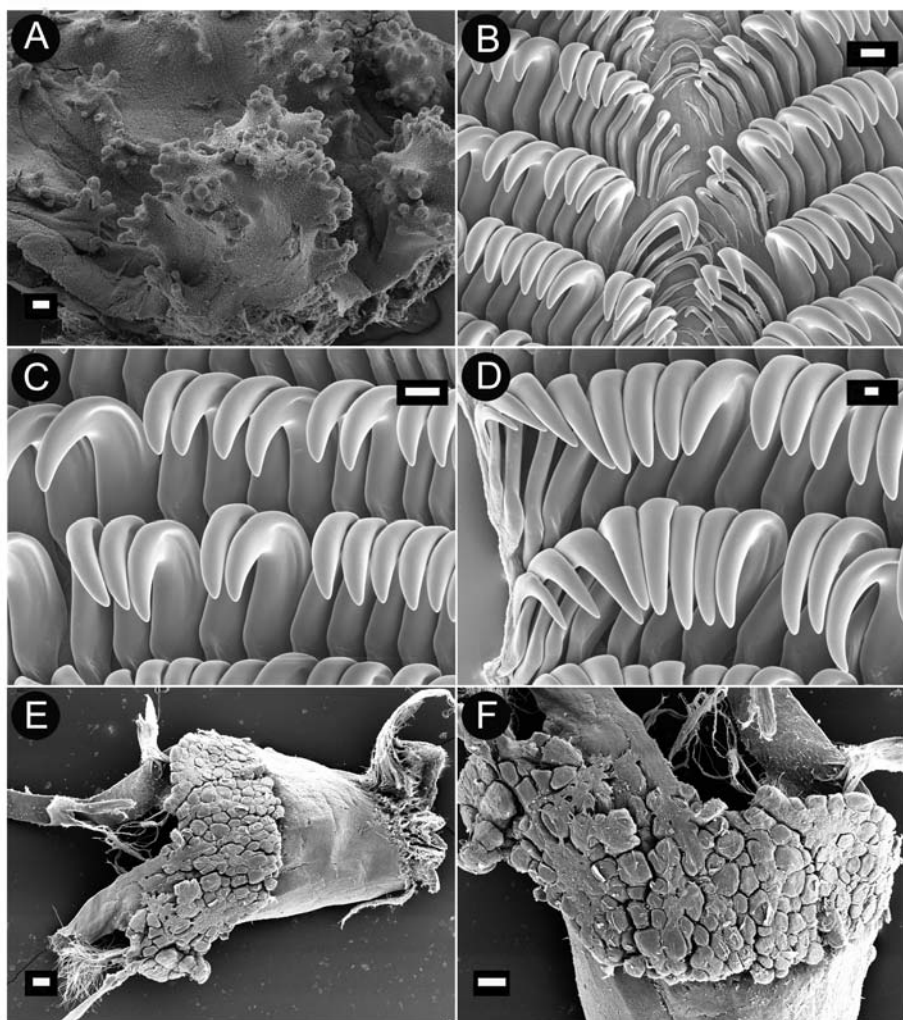


Figure 2. Scanning electron micrographs of *Atagema notacristata* sp. nov. (A) Mantle (MZUCR-INB0003836262), scale bar = 100  $\mu$ m. (B) Innermost radular teeth (MZUCR-INB0003118068, scale bar = 30  $\mu$ m). (C) Midlateral radular teeth (MZUCR-INB0003118068), scale bar = 30  $\mu$ m. (D) Outermost radular teeth (MZUCR-INB0003118068), scale bar = 10  $\mu$ m. (E) Buccal bulb with anterior blood gland (MZUCR-INB0003572319), scale bar = 100  $\mu$ m. (F) Detail of the blood gland, scale bar = 100  $\mu$ m.

The color of the living animal varies from cream to reddish brown (Fig. 1A). There are several dark brown to reddish brown spots over the entire notum that, in some specimens, are bigger and more aggregated near the midline of the dorsum. The tubercles, rhinophores, and branchial leaves also vary from light brown to reddish brown. The apices of the rhinophores and gills are cream to light brown with minute, densely aggregated white specks. Ventrally, the foot is light brown.

**Anatomy.**—The internal anatomy of *A. notacristata* is shown in Figure 3B. There are three pairs of strong buccal retractor muscles attached to the body wall (Fig. 3C). At the buccal end of these systems, there is a conspicuous blood gland composed



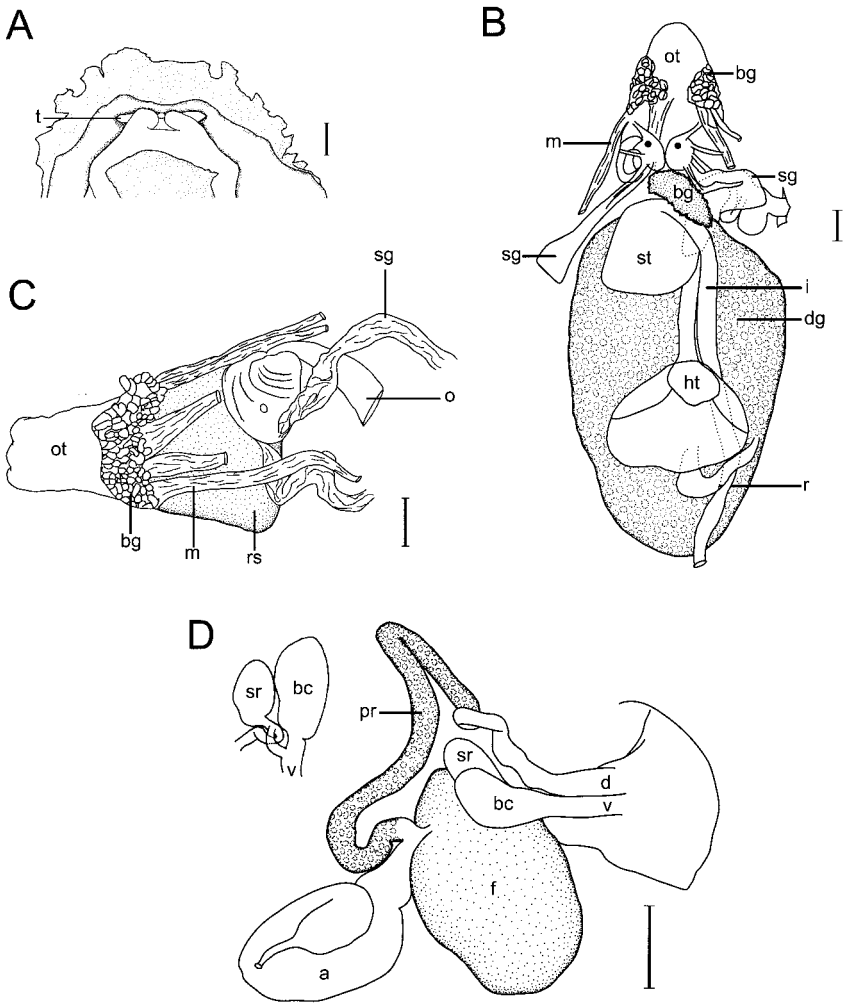


Figure 3. Anatomy of *Atagema notacristata* sp. nov. (A) Ventral view of the mouth area, scale bar = 1 mm (MZUCR-INB0003572297). (B) Dorsal view of the internal organs, scale bar = 1 mm (MZUCR-INB0003572319). (C) Buccal bulb, scale bar = 1 mm. (D) Reproductive system, scale bar = 1 mm (MZUCR-INB0003572319). Abbreviations: a, ampulla; bc, bursa copulatrix; bg, blood gland; d, deferent duct; dg, digestive gland; f, female gland; ht, heart; i, intestine; m, muscles; o, oesophagus; ot, oral tube; pr, prostate; r, syrinx; rs, radular sac; sg, salivary gland; sr, seminal receptacle; st, stomach; t, tentacle; v, vagina.

of many lobules (Figs. 3B, 2E,F). A pair of elongated salivary glands connects to the buccal bulb at each side of the oesophagus (Fig. 3B, C). The buccal bulb is large and wide. The labial cuticle lacks jaw elements. The radular formula is  $15 \times (26.0.26)$  in a 12 mm preserved length specimen (MZUCR-INBI03118068) and  $16 \times (22.0.22)$  in a 14 mm preserved length specimen (MZUCR-INBI03572307). Rachidian teeth are absent. The innermost lateral teeth are thinner and pointed, some less angular and almost plate-like (Fig. 2B). The midlateral teeth are hamate, smooth, and have a single cusp (Fig. 2C). The lateral teeth increase in size gradually towards the medial

portion of the half-row. The outermost teeth are smaller. All the lateral teeth lack denticles (Fig. 2D). The oesophagus is long with a distinct fold onto itself and gradually expands inserting directly into the exposed stomach (Fig. 3C).

The ampulla is very large, wide, and convoluted. It branches into a short oviduct and the prostate. The oviduct enters the female gland mass at its proximal end. The narrow prostate is tubular, long, and granular (Fig. 3D). It connects to a short deferent duct that is about the same width as the prostate. The deferent duct then opens into a common atrium with the vagina. There are no penial hooks. The vagina is short and the same width as the deferent duct. At the end of the vagina, it connects to a pear-shaped bursa copulatrix. The short seminal duct leaves the vagina close to the bursa copulatrix. About half way along its length the insemination duct exits and in a short distance, enters the female gland mass. The bursa copulatrix is slightly larger than the seminal receptacle (Fig. 3D).

*Remarks.*—Valdés and Gosliner (2001) considered the species *Doris ornata* Ehrenberg, 1831, and *Doris intecta* Kelaart, 1858, as synonyms and transferred *D. ornata* to the genus *Atagema* based on the external and internal features of the species. This species differs from *A. notacristata* sp. nov. in external coloration and anatomy. The background of *A. ornata* is dark brown with a wide, whitish line down the dorsal midline that extends from behind or just in front of the rhinophores to the gills. This line varies in color from white to cream and is located on a raised tuberculate crest. The background color of *A. notacristata* is light cream to brown with some minute brown spots that are sometimes more aggregated near the midline of the dorsum. This species lacks the conspicuous dorsal white line. *Atagema ornata* also differs from *A. notacristata* by having outermost teeth that are more elongated and hook-shaped than those of the latter. In addition, in the reproductive system of *A. ornata*, the deferent duct and oviduct are much longer than those of *A. notacristata*.

The only Pacific species, *Atagema alba* (O'Donoghue, 1927), which is found from California to Baja California, can be distinguished from *A. notacristata* by its white background color with small black-gray spots, a higher central tubercle, and triangular, auriform oral tentacles (Bertsch and Gosliner, 1986; Behrens and Hermosillo, 2005). In contrast, *A. notacristata* has a brown background color with no dark spots, highly elevated rhinophoral sheaths, more conical tentacles, and a prominent mid-dorsal ridge.

*Atagema rugosa* and *Atagema gibba*, two species first described by Pruvot-Fol (1951), differ from *A. notacristata* in external morphology and internal anatomy. *Atagema rugosa*, which is found in the Mediterranean (Perrone, 1983a,b) and South Africa (Gosliner, 1987), can be distinguished by its six tripinnate branchial leaves, a smaller median ridge on the dorsum, and a white background with large black spots organized into two longitudinal lines on the sides of the dorsum (see Gosliner, 1987). These black spots can also be found in front of the gills and behind the rhinophores (Perrone, 1983a). *Atagema gibba*, which is found from England to the Mediterranean and South Africa (Gosliner, 1987), can be distinguished by its crenulated mantle edge, tubercles on the dorsum that are not uniformly arranged, smooth brown areas near the mantle edge, five lobes around the branchial sheath, and teeth with a noticeable dark base. In contrast, *A. notacristata* is a light brown dorid lacking black spots on the dorsum, and with five tripinnate branchial leaves, three lobes around the gill, and very distinctive large tubercles uniformly arranged on the notum.

*Atagema browni* Thompson, 1980, found in the Caribbean of Costa Rica, the Cayman Islands, and Jamaica (Valdés et al., 2006), differs from *A. notacristata* externally by having a gray-brown background color with six brown spots dorsally, tubercles that form greatly elevated aggregations on the prominent longitudinal ridge, and re-curved oral tentacles.

*Doris prea* (Marcus and Marcus, 1967), from Florida and the Caribbean, could potentially be confused with our species based on external appearance. However, it differs from *A. notacristata* in having a dorsum with tubercles but no caryophyllidia, a cream-brown background, a mid-dorsal longitudinal depression with black patches lacking tubercles, and seven tripinnate branchial leaves. In contrast, *A. notacristata* has tubercles with caryophyllidia, a light brown dorsum lacking black patches, a branchial sheath composed of three lobes in the anterior border, and five tripinnate branchial leaves.

### Genus *Geitodoris* Bergh, 1891

*Geitodoris* Bergh, 1891: 130. Type species: *Doris complanata* Verrill, 1880, by monotypy.

#### *Geitodoris mavis* (Marcus and Marcus, 1967)

(Figs. 1B, 4A–G, 5A–C)

*Discodoris mavis* Marcus and Marcus, 1967: 187–189, fig. 46

*Geitodoris mavis* Schrödl, 2000: 208

*Material Examined*.—Playa Avellanas, Guanacaste, Costa Rica (10°13'28"N, 85°50'26"W), 21 April 2004, 1 specimen (dissected), 15 mm preserved length, intertidal, leg. T. Gosliner (MZUCR-INB0003836290); East side of Isla Ballena, Parque Nacional Marino Ballena, Puntarenas, Costa Rica (9°06'24"N, 83°43'35"W), 16 January 2000, 6 specimens (1 dissected), 3–11 mm preserved length, 6 m depth, leg. M. Calderón (MZUCR-INB0001496571); 500 m. W of Punta Carbón, Playa Grande, Guanacaste, Costa Rica (10°20'59"N, 85°51'55"W), 11 January 2001, 1 specimen (dissected), 10 mm preserved length, intertidal, leg. S. Ávila (MZUCR-INB0003117991); Punta Uvita, Parque Marino Ballena, Puntarenas, Costa Rica (9°08'50"N, 83°45'47"W), 15 January 2003, 10 specimens, 4–10 mm preserved length, intertidal, leg. A. Valdés (MZUCR-INB0003572302); E side of Isla Ballena, Parque Nacional Marino Ballena, Puntarenas, Costa Rica (9°06'26"N, 83°43'39"W), 17 January 2000, 9 specimens, 3–10 mm preserved length, 7 m depth, leg. M. Calderón (MZUCR-INB0001496557); Puerto Escondido, Parque Nacional Manuel Antonio, Puntarenas, Costa Rica (9°23'02"N, 84°08'14"W), 18 February 2003, 1 specimen, 5 mm preserved length, intertidal, leg. Y. Camacho (MZUCR-INB0003572317); 25 km SW from San Pedrillo Station, Parque Nacional Corcovado, Puntarenas, Costa Rica (8°36'40"N, 83°44'16"W), 21 January 2000, 2 specimens, 5–6 mm preserved length, intertidal, leg. M. Calderón (MZUCR-INB0001496533); Punta Uvita, Parque Nacional Marino Ballena, Puntarenas, Costa Rica (9°08'44"N, 83°45'33"W), 15 January 2000, 11 specimens (1 dissected), 5–12 mm preserved length, intertidal, leg. M. Calderón (MZUCR-INB0001496173); Punta Uvita, Parque Nacional Marino Ballena, Puntarenas, Costa Rica (9°08'50"N,

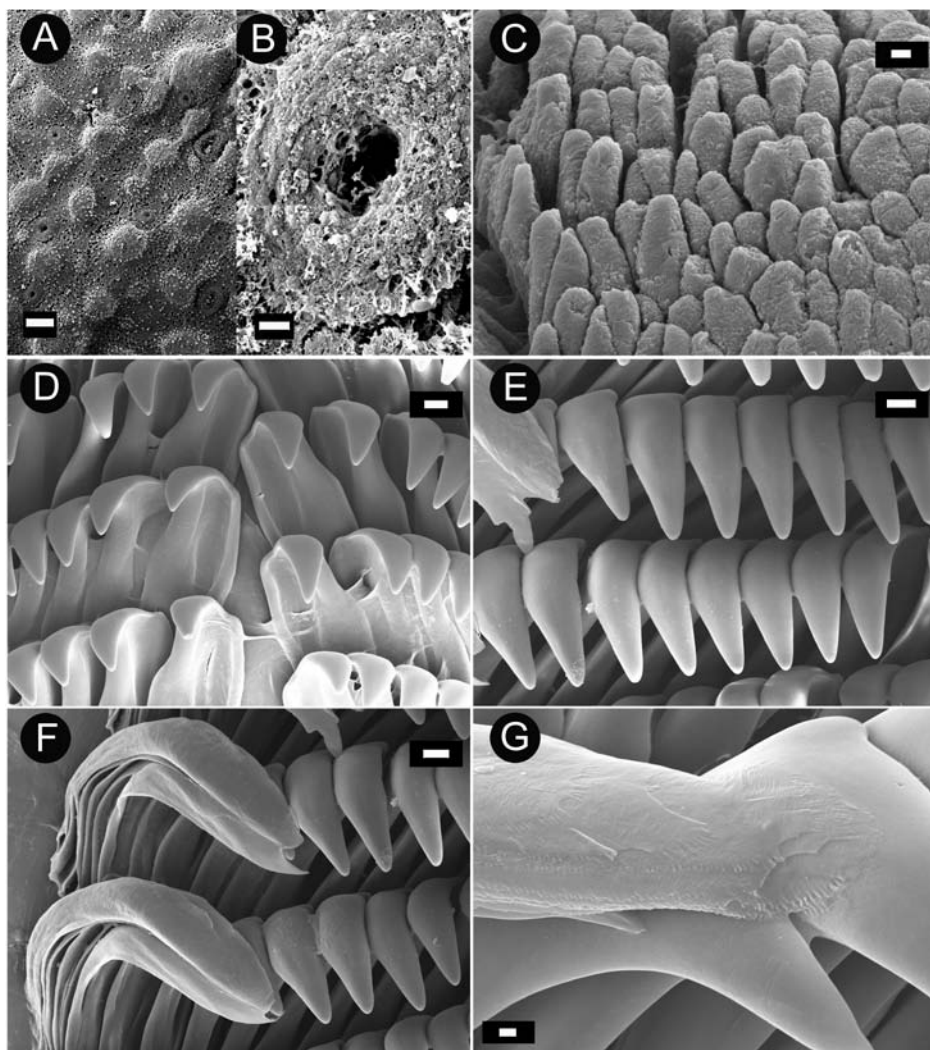


Figure 4. Scanning electron micrographs of *Geitodois mavis*, (A) Mantle (MZUCR-INB0003572301), scale bar = 100  $\mu$ m. (B) Detail of mantle hole (MZUCR-INB0003572301), scale bar = 10  $\mu$ m. (C) Jaw elements (MZUCR-INB00014966173), scale bar = 3  $\mu$ m. (D) Innermost radular teeth (MZUCR-INB00014966173), scale bar = 10  $\mu$ m. (E) Midlateral radular teeth (MZUCR-INB00014966173), scale bar = 10  $\mu$ m. (F) Outermost radular teeth (MZUCR-INB00014966173), scale bar = 10  $\mu$ m. (G) Detail of the outermost teeth (MZUCR-INB00014966173), scale bar = 2  $\mu$ m.

83°45'47"W), 15 January 2003, 7 specimens (1 dissected), 4–10 mm preserved length, 0–1 m depth, leg. A. Valdés (MZUCR-INB0003572301).

**Distribution.**—Thus far, this species is only known from the Pacific coasts of Mexico, Costa Rica, and the Galápagos Islands (Camacho-García et al., 2005).

**External Morphology.**—The body is oval to elongate (Fig. 1B). There are no caryophyllidia on the dorsum. The dorsum is completely covered in smooth, round, densely distributed tubercles, with some larger than others (Fig. 4A). In some of the larger specimens, the larger conical tubercles are arranged in a longitudinal keel along the mid-dorsum that extends from behind the rhinophores to the branchial sheath. The



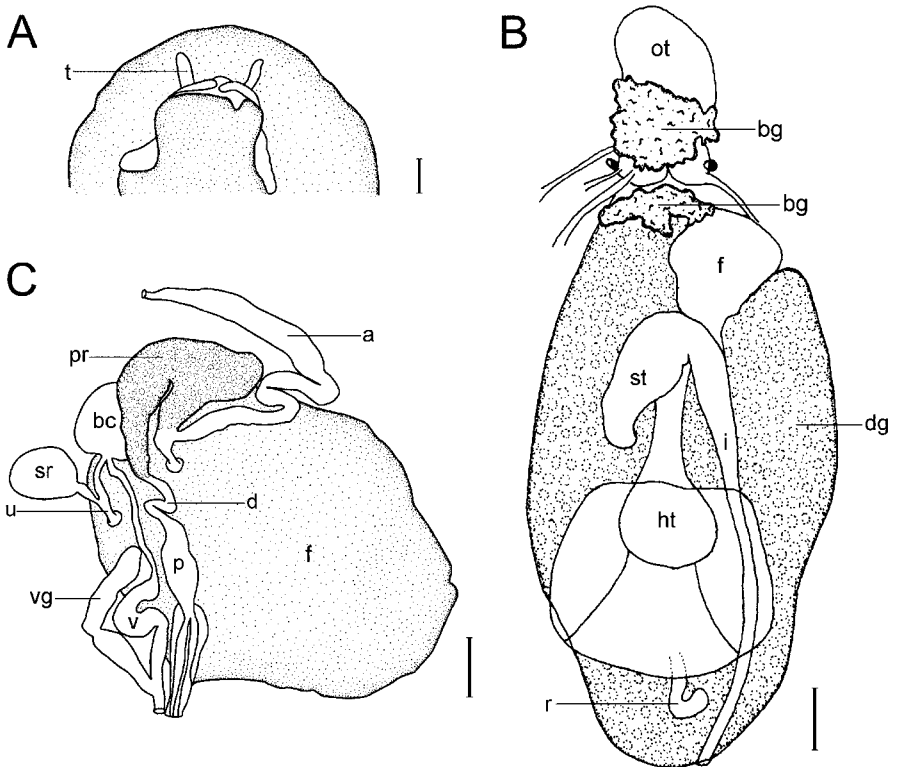


Figure 5. Anatomy of *Geitodoris mavis*. (A) Ventral view of the mouth area, scale bar = 1 mm (MZUCR-INB0003117991). (B) Dorsal view of the internal organs scale bar = 1 mm (MZUCR-INB0003836290). (C) Reproductive system (MZUCR-INB0003572301), scale bar = 1 mm. Abbreviations: a, ampulla; bc, bursa copulatrix; bg, blood gland; d, deferent duct; dg, digestive gland; f, female gland; ht, heart; i, intestine; ot, oral tube; p, penis; pr, prostate; r, syrinx; sr, seminal receptacle; st, stomach, t, tentacle; u, uterine duct; v, vagina; vg, vestibular gland.

entire mantle is covered in minute holes or cutaneous glands, approximately 20  $\mu\text{m}$  in diameter, which are homogeneously distributed (Fig. 4B). The function of these glands is unknown. There are 13 lamellae on each rhinophore of an 8 mm preserved length specimen (MZUCR-INBI0003572302) and 11 lamellae in a 7 mm preserved length specimen (MZUCR-INBI0003572302). There are eight tripinnate branchial leaves. The oral tentacles are digitiform in shape (Fig. 5A). Ventrally, the foot is notched and grooved.

The background color is variable, ranging from light yellow to light orange, the dorsum normally darker and the margin lighter (Fig. 1B). There are several minute brown spots aggregated around the mantle holes. Both brown and orange tubercles cover the dorsum, although there are fewer brown tubercles. There are also opaque white tubercles distributed in a longitudinal line from behind the rhinophores to the gills in some specimens. The rhinophores are light yellow with numerous opaque white and brown spots. The rhinophoral apex and edge of the branchial sheath is opaque white. The branchial leaves are light yellow with numerous minute brown spots. The apex of the anal aperture is darker. Ventrally, the foot is light yellow with no spots.

**Anatomy.**—The labial cuticle has irregular jaw elements (Fig. 4C). The radular formula is  $18 \times (25.0.25)$  in a 9 mm preserved length specimen (MZUCR-INB0001496173) and  $21 \times (32.0.32)$  in a 10 mm preserved length specimen (MZUCR-INB0001496173). Rachidian teeth are absent. The innermost teeth are hamate with a wide and almost rectangular base, and they lack denticles (Fig. 4D). The midlateral teeth are hamate, with a prolongation on the upper side (Fig. 4E). The lateral teeth increase in size gradually towards the medial portion of the half-row. The outermost teeth are leaf-like with numerous minute denticles (Fig. 4F,G). The stomach has a pear-like shape and connects distally to the long intestine, which runs to the anal opening (Fig. 5B).

The ampulla is very long and convoluted in the middle portion (Fig. 5C). It branches into a long oviduct and the prostate. The thick prostate is muscular and convoluted. The deferent duct is distal to the prostate. It is long, wider in the middle portion and opens into a prostate. The proximal end of the deferent duct opens into a common atrium with the vagina. The vagina is long and tubular in shape with a loop in the middle portion. Its proximal part connects to a wide and tubular vestibular gland, and at its distal end, to the large and oval bursa copulatrix. From the bursa copulatrix leads a separate short seminal duct that connects to the oval seminal receptacle. The short insemination duct splits off about half way along its length to enter the female gland mass (Fig. 5C). The seminal receptacle is slightly smaller than the bursa copulatrix.

**Remarks.**—Schrödl (2000) transferred the species *D. mavis* into the genus *Geitodoris* based on the presence of pectinate outermost teeth. *Geitodoris mavis* differs from other congeners in its external morphology and anatomy.

*Geitodoris pusae*, a species described by Marcus (1955) from Florida, Brazil, Jamaica, Martinique and Costa Rica (Valdés et al., 2006), is different from *G. mavis* due to the presence of five spicules in the vestibular gland and by having a background color that is pink to pale brown with dark brown spots on the notum (Thompson, 1980; Ortea et al., 1988). The background color of *G. mavis* ranges from light yellow to light orange, with no dark spots. In addition, this species lacks the spicules or cuticular spines in the vestibular gland.

Two other Pacific species, *Geitodoris heathi* (MacFarland, 1905) from California and *Geitodoris patagonica* Odhner, 1926, from Argentina and Chile (Schrödl, 2000) differ from *G. mavis*. The former species has a white to pale yellow background with some dark brown spots, nine tripinnate branchial leaves, and a nearly smooth granular dorsum. The latter species differs from *G. mavis* by possessing a whitish notum with irregular black spots, seven to eight bipinnate branchial leaves, and the presence of smooth, irregularly-worn marginal teeth (Schrödl, 2000). *Geitodoris mavis* has tubercles densely arranged on the notum, pectinate, denticulate outermost teeth, and eight to ten tripinnate branchial leaves.

The identity of *Geitodoris immonda*, a species described by Bergh (1894) from the Caribbean and the Eastern Pacific and recently reported to be found in Costa Rica, Venezuela, and Brazil by Valdés et al. (2006), will be addressed in detail in a revision of the genus *Geitodoris*. The type material of *G. immonda* is lost and thus the best is to regard the species as a *nomen dubium* (B. Dayrat, University of California at Merced, pers. comm.).

The study of several specimens from Costa Rica and the review of the original description confirm that the external and internal features of this species fit with the description of *G. mavis*.

## Family DORIDIDAE Rafinesque, 1815

Genus *Doris* Linnaeus, 1758: 653. Type species: *Doris verrucosa* Linnaeus, 1758, by monotypy.

*Doris immonda* (Risbec, 1928)

(Figs. 1C, 6A–D, 7A–C)

*Platydoris immonda* Risbec, 1928: 84, pl. 1. fig. 4, text fig. 12.

*Material Examined.*—Playa Avellanas, Guanacaste, Costa Rica (10°13'28"N, 85°50'26"W), 21 April 2004, 1 specimen (dissected), 15 mm preserved length, intertidal, leg. T. Gosliner (MZUCR-INB0003836289); Tengan Pier, 14 km W of Ikei-Shima, Okinawa, Ryukyu Islands, Japan, 20 March 1993, 1 specimen (previously dissected), 21 mm preserved length, 12 m depth, leg R. Bolland (CASIZ089023).

*Distribution.*—This species is found in the tropical Indo-Pacific (Brodie and Willan, 1993), Australia and Japan (Rudman, 2000), and Costa Rica (Camacho-García et al., 2005).

*External Morphology.*—The body is oval and the dorsum is covered with numerous conical tubercles (Fig. 1C), which are larger towards the center of the notum (Fig. 6A). Some of these tubercles aggregate, forming a longitudinal keel that extends from behind the rhinophores to the anterior part of the branchial leaves. There are five tripinnate branchial leaves and 15 lamellae in the rhinophores. The rhinophoral sheaths have one posterior and two large lateral tubercles (Fig. 7A). Similar tubercles (to the rest of the notum) surround the branchial sheath. Ventrally, the oral tentacles are reduced, forming two auriculate prolongations on each side of the mouth aperture (Fig. 7B). The anterior portion of the foot is grooved but not notched.

The background color of the living animal is dark orange with some greenish and brownish patches. The dorsum has an opaque white to brown patch resembling an inverted Y, and composed of tubercles with brownish tips. The tubercles in the middle part are greenish to brown in color. The perfoliate rhinophores are yellowish cream with numerous little brown spots. The branchial leaves are light orange, however, the exterior margins of the branchial leaves are opaque white. The ventral side of the foot is light orange without spots.

*Anatomy.*—The labial cuticle is smooth. The radular formula is  $48 \times (67.0.67)$  in a 15 mm preserved-length specimen. There are no rachidian teeth. The innermost teeth are hamate, pointed, and lack denticles (Fig. 6B). The midlateral teeth are also hamate, pointed, and smooth (Fig. 6C). The five outermost teeth are wide and pectinate (Fig. 6D).

The ampulla is very wide, long, and convoluted in the middle portion (Fig. 7C). The short oviduct enters the female gland mass in the mid-upper area. The prostate is very short and thin, and almost undifferentiated from the deferent duct. The deferent duct is also short and tubular and opens into a common atrium with the vagina. The penis is unarmed. The vagina is short, tubular, and bends slightly before entering the bursa copulatrix. From the bursa copulatrix a separate seminal duct leads to the seminal receptacle. About half way along its length, a long, thin, uterine duct branches off to

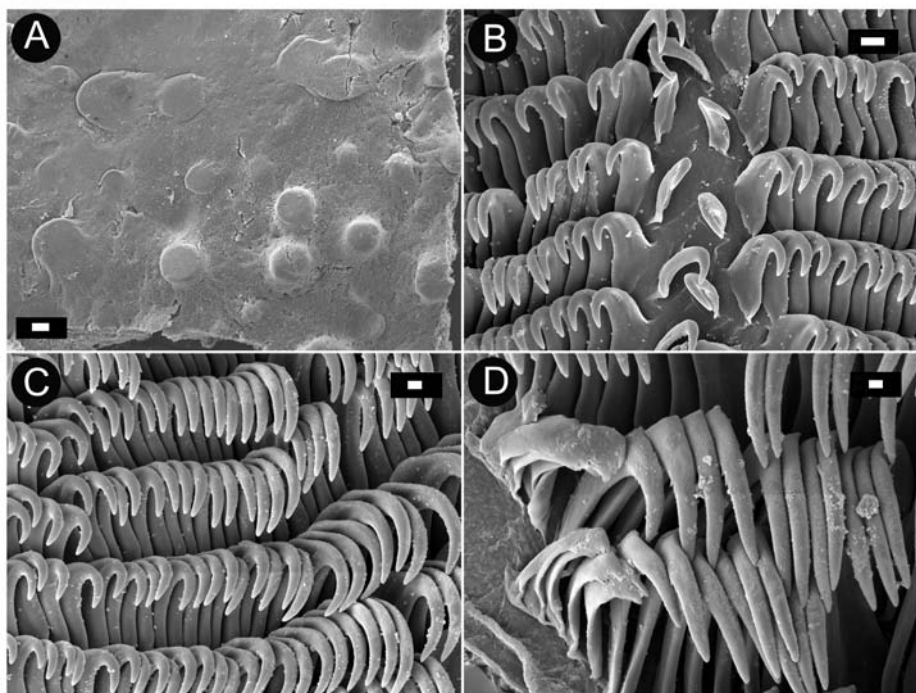


Figure 6. Scanning electron micrographs of *Doris immonda* (MZUCR-INB0003836289). (A) Mantle, scale bar = 100  $\mu$ m. (B) Innermost radular teeth, scale bar = 30  $\mu$ m. (C) Midlateral radular teeth, scale bar = 10  $\mu$ m. (D) Outermost radular teeth, scale bar = 10  $\mu$ m.

enter the distal part of the female gland mass. The oval bursa copulatrix is five times the size of the seminal receptacle (Fig. 7C).

*Remarks.*—There has been much confusion surrounding this species. Brodie and Willan (1993) identified this species as *Siraius nucleola* (Pease, 1860) and considered *Doris carinata* Alder and Hancock, 1864, a synonym. They transferred this species from *Doris* to *Siraius* based on the presence of pectinate outer teeth. Valdés (2002) considered *Siraius* a synonym of *Doris* since there is variability in the presence or absence of pectinate outer lateral teeth within several dorid genera.

Rudman (2000) in the Seaslug Forum, doubted Brodie and Willan's identification as well as that of Kay and Young (1969). He described several inconsistencies in Pease's and Alder and Hancock's descriptions. We agree with Rudman that this species should be identified as Risbec's (1928) description of *P. immonda* that it should be placed in the genus *Doris*. Rudman suggested that further speculation regarding the identification of Kay and Young's material must await examination of new material from Hawaii. While we agree with this statement the external and internal morphology they described is consistent with that of *D. immonda*.

Valdés (2002) redescribed *D. immonda* from new material collected in Japan. The main distinctive features reported were the presence of an "inverted Y" pattern extending mid-dorsally from between the rhinophores to the gill; tubercles on the dorsum (the largest ones situated in the central region of the body); rhinophoral sheaths with tubercles; five tripinnate branchial leaves; two blunt oral tentacles on each side of the mouth opening; and a grooved, but not notched, anterior border of the foot.



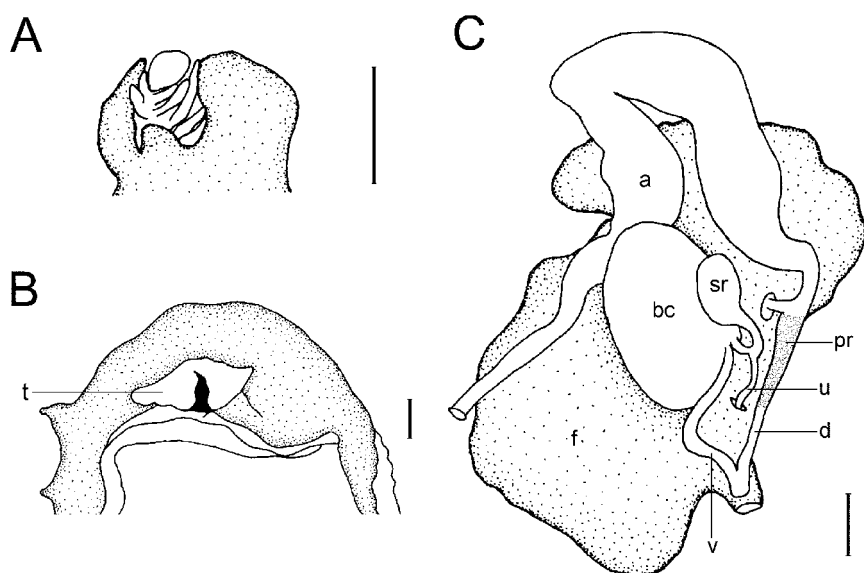


Figure 7. Anatomy of *Doris immonda* (MZUCR-INB0003836289). (A) Detail of the rhinophore, scale bar = 1 mm. (B) Ventral view of the mouth area, scale bar = 1 mm. (C) Reproductive system, scale bar = 1 mm. Abbreviations: a, ampulla; bc, bursa copulatrix; t, tentacular prolongation; d, deferent duct; f, female gland; pr, prostate; sr, seminal receptacle; u, uterine duct; v, vagina.

The only specimen collected from the Pacific Coast of Costa Rica fits with this description. In addition, the external coloration of the specimen from Costa Rica is similar to that of the specimen from Japan as described by Valdés (2002). This species can be distinguished from other congeners found in Costa Rica by the external coloration and an “inverted Y” on the dorsum. This is the first record of the species for the tropical eastern Pacific. The eastern Pacific is likely part of its natural range, as there are other Western Pacific species that are found in the eastern Pacific such as *Haminoea ovalis* Pease, 1868 (Camacho-García et al., 2005), and *Embletonia gracilis* Risbec, 1928 (Hermosillo et al., 2006).

*Doris pickensi* Marcus and Marcus, 1967

(Figs. 1D, 8A–D, 9A–C)

*Doris pickensi* Marcus and Marcus, 1967: 184–186, fig. 45

**Material Examined.**—Punta Gringa, off rock on NE side of point, Bahía de los Angeles, Gulf of California, Baja California Norte, Mexico, 1–3 October 1984, 2 specimens (1 dissected), 7–9 mm preserved length, 4–4.5 m depth, leg. R. Van Syoc (CASIZ 057345); Punta Gringa, off rock on NE side of point, Bahía de los Angeles, Gulf of California, Baja California Norte, Mexico, 2 October 1984, 1 specimen (dissected), 5 mm preserved length, 3–4.5 m depth, leg. T. Gosliner (CASIZ 072931); Playa Manzanillo, Isla Golfo de San Lucas, Puntarenas, Costa Rica (9°56′03″N, 84°54′52″W), 9 December, 1999, 2 specimens (dissected), 3–4 mm preserved length,

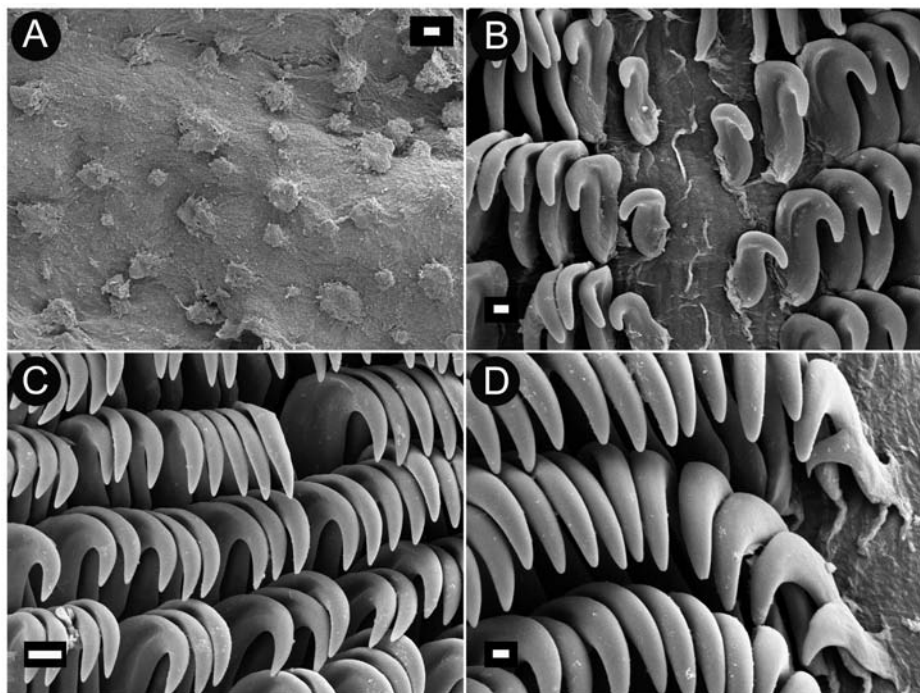


Figure 8. Scanning electron micrographs of *Doris pickensi*. (A) Mantle (MZUCR-INB0001496652), scale bar = 30  $\mu$ m. (B) Innermost radular teeth. (MZUCR-INB0003572541), scale bar = 3  $\mu$ m. (C) Midlateral radular teeth (MZUCR-INB0003572541), scale bar = 10  $\mu$ m. (D) Outermost radular teeth (MZUCR-INB0003572541), scale bar = 3  $\mu$ m.

2 m depth, leg. M. Calderón (MZUCR-INB0001496624); In front of the tidepool, San Miguel Station, Reserva Natural Absoluta de Cabo Blanco, Puntarenas, Costa Rica (9°34'50"N, 85°08'26"W), 26 January 1999, 2 specimens (dissected), 3–5 mm preserved length, intertidal, leg. F. Alvarado (MZUCR-INB0001496657); Punta Flor, Cabuya Station, Reserva Natural Absoluta de Cabo Blanco, Puntarenas, Costa Rica (9°34'28"N, 85°05'29"W), 13 January 1997, 1 specimen (dissected), 6 mm preserved length, 10 m depth, leg. Y. Camacho (MZUCR-INB0001496652); Peñón del Coral, Playa Coralito, Puntarenas, Costa Rica (9°39'52"N, 85°11'32"W), 29 January 1999, 2 specimens (dissected), 4–5 mm preserved length, intertidal, leg. F. Alvarado (MZUCR-INB0001496270); Isla Copey, Puntarenas, Costa Rica (8°43'40"N, 83°23'28"W), 19 February 1997, 1 specimen (dissected), 4 mm preserved length, 9 m depth, leg. S. Ávila (MZUCR-INB0003701267); Punta Uvita, Parque Nacional Marino Ballena, Puntarenas, Costa Rica (9°08'50"N, 83°45'47"W), 15 January 2003, 1 specimen (dissected), 5 mm preserved length, intertidal, leg. A. Valdés (MZUCR-INB0003572541); 2 km SW from San Pedrillo Station, Puntarenas, Costa Rica (8°36'53"N, 83°44'18"W), 20 January 2000, 1 specimen (dissected), 5 mm preserved length, intertidal, leg. M. Calderón (MZUCR-INB0001496424).

**Distribution.**—This species is found from the Gulf of California to Costa Rica (Camacho-García et al., 2005).

**External Morphology.**—The body is oval and elongate (Fig. 1D). The dorsum is covered in rounded tubercles (Fig. 8A) of different sizes, with the larger ones in the central part of the notum. There are similar tubercles in the rhinophoral and bran-

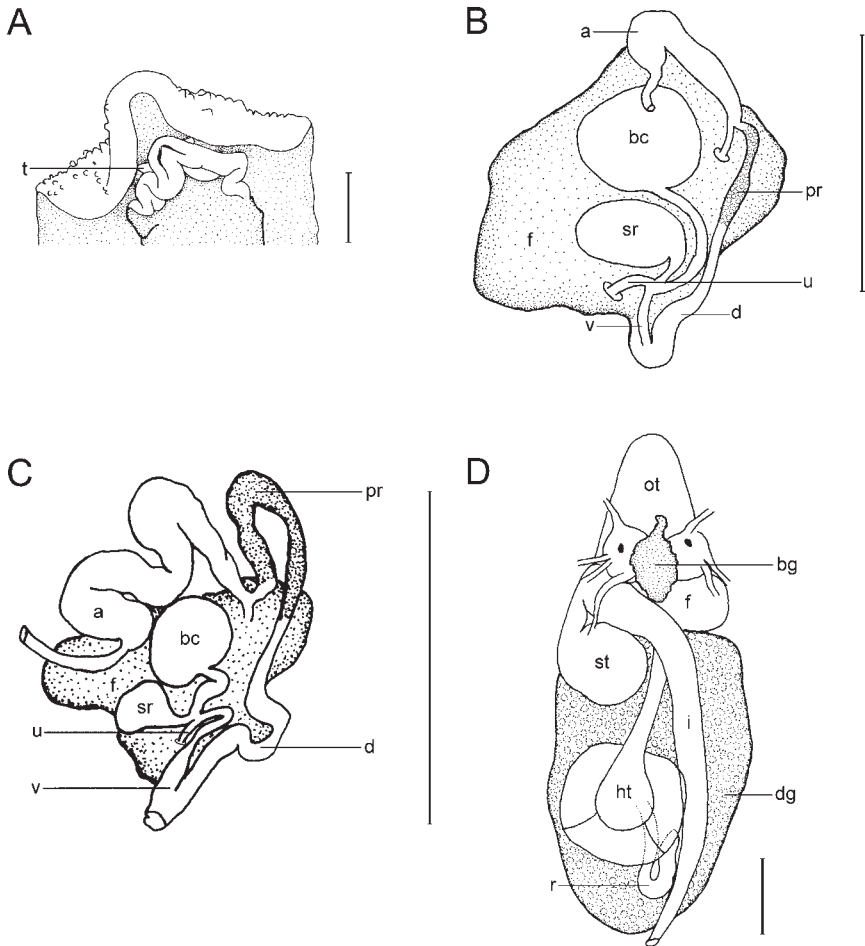


Figure 9. Anatomy of *Doris pickensi*. (A) Ventral view of the mouth area, scale bar = 1 mm (MZUCR-INB0003572541). (B) Reproductive system (MZUCR-INB0001496657), scale bar = 1 mm. (C) Reproductive system (CASIZ 057345), scale bar = 1 mm. (D) Dorsal view of the internal organs (MZUCR-INB0001496652), scale bar = 1 mm. Abbreviations: a, ampulla; bc, bursa copulatrix; d, deferent duct; dg, digestive gland; f, female gland; ht, heart; i, intestine; ot, oral tube; pr, prostate; r, syrinx; sr, seminal receptacle; st, stomach; t, tentacle; u, uterine duct; v, vagina.

chial sheaths. The mantle is covered in spicules. The tubercles also have spicules that project on the surface. The rhinophores have 13 lamellae in a 9 mm preserved length specimen (CASIZ057345) and 12 lamellae in the rhinophores in a 6 mm preserved length specimen (MZUCR-INB01496652). The gill consists of 10 (MZUCR-INB01496652) or 11 (CASIZ057345) unipinnate branchial leaves. There are blunt digitiform oral tentacles (Fig. 9A). The anterior border of the foot is grooved but not notched.

The background color of the dorsum in the living animal is translucent white to cream or light yellow to orange (Fig. 1D). There are a few minute brown spots on the dorsum. The rhinophores and branchial leaves are yellow or cream in color. The viscera are visible through the mantle. Ventrally, the foot is translucent white.

*Anatomy.*—The labial cuticle is smooth. The radular formula of a 4 mm preserved length specimen is  $22 \times (25.0.25)$  (MZUCR-INB001496624) and of a 5 mm preserved length specimen is  $28 \times (33.0.33)$  (MZUCR-INB0003572541). In general, the teeth are broad and hook-shaped. The innermost teeth are wide and angular (Fig. 8B). All lateral teeth are smooth (Fig. 8C,D). They gradually become larger from the innermost to the mid-laterals, then become smaller and less angular from the mid-laterals to the outermost (Fig. 8C,D). The oesophagus is large and tubular and connects to an exposed, rounded stomach (Fig. 9D).

The ampulla is located in the distal right part of the female gland (Fig. 9B,C). The prostate is granular, straight, and of nearly uniform width. It leads to a tubular deferent duct that can be either straight or looped. In some of the specimens from Costa Rica (Fig. 9B) and Baja California (Fig. 9C), the prostate is almost undifferentiated from the deferent duct. In contrast to the condition found by Marcus and Marcus (1967), these specimens show a highly unusual, vaginal arrangement of ducts: the duct to the seminal receptacle and the uterine duct both leave the vagina separately but next to each other (Fig. 9B,C). The penis is unarmed. The bursa copulatrix is nearly spherical; from it, leads another thin duct that connects to an oval seminal receptacle and a short uterine duct. The bursa copulatrix is twice the size of the seminal receptacle (Fig. 9B,C).

*Remarks.*—Marcus and Marcus (1967) described this species based on several specimens from Sonora, Mexico. They reported that this species can be easily distinguished from other members of the genus by the following characters: external coloration, which in most specimens is white to cream with some small brown spots on the notum; dorsum with low tubercles and spicules; 13–14 unipinnate branchial leaves; and a grooved and sometimes notched anterior border of the foot.

*Doris granulosa* (Pease, 1860), a species reported from the Indo-Pacific, differs from *D. pickensi* by having a pale yellow-orange background, gill branches arranged in a transverse line across the back, and a dorsal flap covering the gill opening. This species has also been reported from the eastern Pacific (Hermosillo et al., 2006), but the identification of this report needs to be confirmed.

*Doris tanya* Marcus, 1971, a species from the eastern Pacific, has a notable pattern of ridges and depressions composed of tubercles of different sizes, features that are not present in *D. pickensi*.

The specimens from Costa Rica and Baja California fit with Marcus and Marcus' description. However, we found some differences in the reproductive system. The prostate is straight, poorly differentiated from the deferent duct, and of nearly uniform width. In addition, in two of the specimens examined from Costa Rica and the two dissected specimens (CASIZ 057345 and CASIZ 072931) from Baja, the duct that leads from the bursa copulatrix is longer than that depicted by Marcus and Marcus (1967; fig. 45c) and joins the seminal receptacle at its distal end. The poor preservation of the specimens and the immature stage of the reproductive system prohibited us from confirming this condition in all specimens from Costa Rica.



*Doris tanya* Marcus, 1971

(Figs. 1E, 10A–D, 11A–D)

*Doris tanya* Marcus, 1971: 357–362; figs. 4–8.*Halgerda* sp. Hertz, 1978: 99; fig. 1.*Sclerodoris tanya* Bertsch, 1981: 217–229; figs. 2–7.

*Material Examined*.—Catalina Channel, California, 18 June 1901, 1 specimen, 60 mm preserved length, leg. W. H. Ritter and W. J. Raymond (CASIZ 067668); Flood Control Channel, Mission Bay, San Diego County, California, 27 March 1974, 1 specimen, 22 mm preserved length, leg. J. Patton (CASIZ 070895); below Centro de Acuacultura, Bahía Tortugas, Baja California Sur, Mexico, 29 June 1984, 1 specimen (dissected), 38 mm preserved length, intertidal, leg. D. Catania (CASIZ 071502); Playa Avellanas, Guanacaste, Costa Rica (10°13'28"N, 85°50'26"W), 21 April 2004, 1 specimen, 18 mm preserved length, intertidal, leg. T. Gosliner (MZUCR-INB0003836280); South Side of Punta Quepos, Puntarenas, Costa Rica (9°23'39"N, 84°10'12"W), 21 November 2000, 2 specimens (1 dissected), 9–12 mm preserved length, 9 m depth, leg. S. Ávila (MZUCR-INB0003118083); 25 km SW from San Pedrillo Station, Parque Nacional Corcovado, Puntarenas, Costa Rica (8°36'40"N, 83°44'16"W), 21 January 2000, 1 specimen, 18 mm preserved length, intertidal, leg. M. Calderón (MZUCR-INB0003701253); Isla Saboga, Panama, 23 February 2001, 1 specimen (dissected), 11 mm preserved length, leg. M. Medina (CASIZ 172355).

*Distribution*.—This species is found from Southern California to Panama (present paper).

*External Morphology*.—The body is oval, elevated, and widest in the middle region (Fig. 1E). The mantle margin is wide and undulate. There are no caryophyllidia on the dorsum. The entire dorsum is covered with large conical composite tubercles of various sizes (Fig. 10A). Each tubercle has several papillae or minute tubercles on the surface. The largest ones are generally located in the middle region of the notum, forming two raised longitudinal rows that extend from the front of the rhinophores to the gills. Each longitudinal row has between seven and nine composite tubercles, with two large ones located at each side of the rhinophoral sheath. There are also some tubercles of different sizes around the branchial sheath. The rhinophores have 30 thin lamellae in a 12 mm preserved length specimen (MZUCR-INBI0003118083) and 24 lamellae in an 18 preserved length specimen (MZUCR-INBI0003836280). The gill consists of seven (MZUCR-INB0003836280) or eight (CASIZ 071502) tripinnate branchial leaves. The oral tentacles are flattened and paddle-shaped (Fig. 11A). The anterior border of the foot is grooved but not notched.

The background color of the dorsum in the living animal is gray-brown with numerous dark brown spots homogeneously distributed around the mantle (Fig. 1E). There are some opaque white spots on some of the tubercles. The base and tips of the rhinophores are light brown, with the remainder a dark grayish cream with numerous minute gray to black spots. The color of the branchial sheaths is light gray with numerous small gray to black spots that are more aggregated in some parts of the gill. There are also some small opaque yellow specks on the gill. The oral tentacles are dark cream with some dark brown spots. The sole of the foot and the hyponotum have a dark cream background with dark brown densely arranged spots.

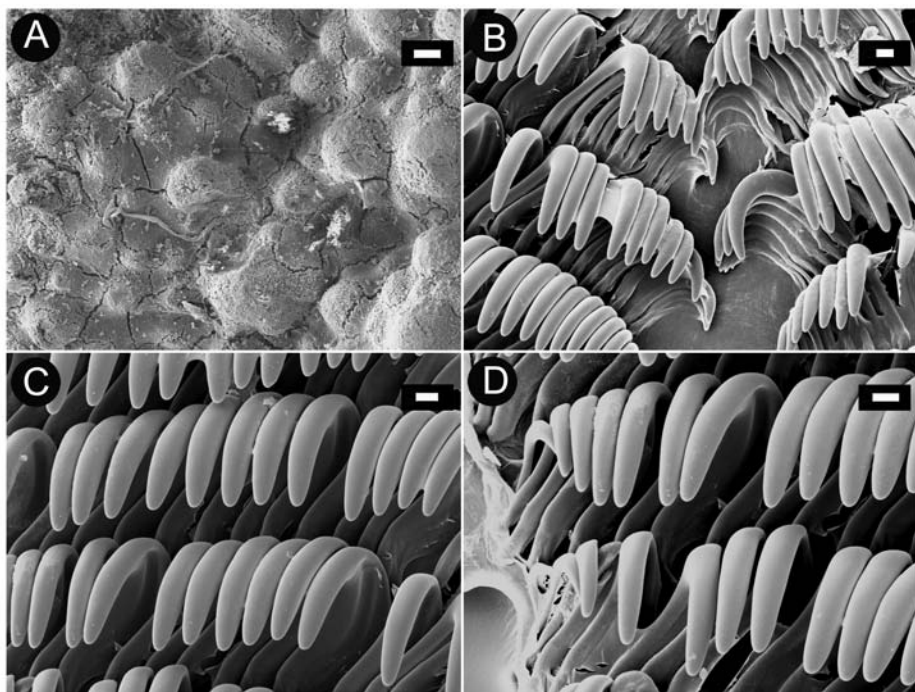


Figure 10. Scanning electron micrographs of *Doris tanya* (MZUCR-INB0003118083). (A) Mantle, scale bar = 100  $\mu\text{m}$ . (B) Innermost radular teeth, scale bar = 10  $\mu\text{m}$ . (C) Midlateral radular teeth, scale bar = 10  $\mu\text{m}$ . (D) Outermost radular teeth, scale bar = 10  $\mu\text{m}$ .

**Anatomy.**—The posterior end of the oral tube has three pairs of strong buccal mass retractor muscles (Fig. 11B) attached to the body wall. There are two salivary glands that connect to the buccal mass under the oesophagus. The labial cuticle is smooth. The radular formula of a 12 mm preserved length specimen is  $18 \times (27.0.27)$  (MZUCR-INB0003118083) and of an 11 mm preserved length specimen is  $17 \times (20.0.20)$  (CASIZ 172355). In general, the teeth are broad and hook-shaped. All lateral teeth are smooth (Fig. 10B,D). They gradually become larger and thicker from the innermost to the mid-laterals, then become smaller and less angular from the mid-laterals to the outermost. The oesophagus is long, wide, tubular, and extends directly into the exposed stomach (Fig. 11C).

The ampulla, which is long and convoluted, is located to the left of the middle of the female gland mass (Fig. 11D). It leads to a granular and convoluted prostate, which is folded upon itself at about its mid-length. The deferent duct is short and coiled. It opens into a common atrium with the vagina. The other seminal duct does not leave from the bursa copulatrix but from the vagina (about 2/3 along its length) and runs to the seminal receptacle. It is a long, thin, wavy duct and the short uterine duct branches off about 2/3 of the way along its path to the seminal receptacle. The penis is unarmed. The long vagina connects to the globular bursa copulatrix, from which emerges another thin and coiled duct that connects to the oval seminal receptacle and the short uterine duct (Fig. 11D).

**Remarks.**—Marcus (1971) described this species as a member of the genus *Doris* based on similarities of the reproductive system, with other species in that genus. Based on the new material from Costa Rica and California, we conclude that this

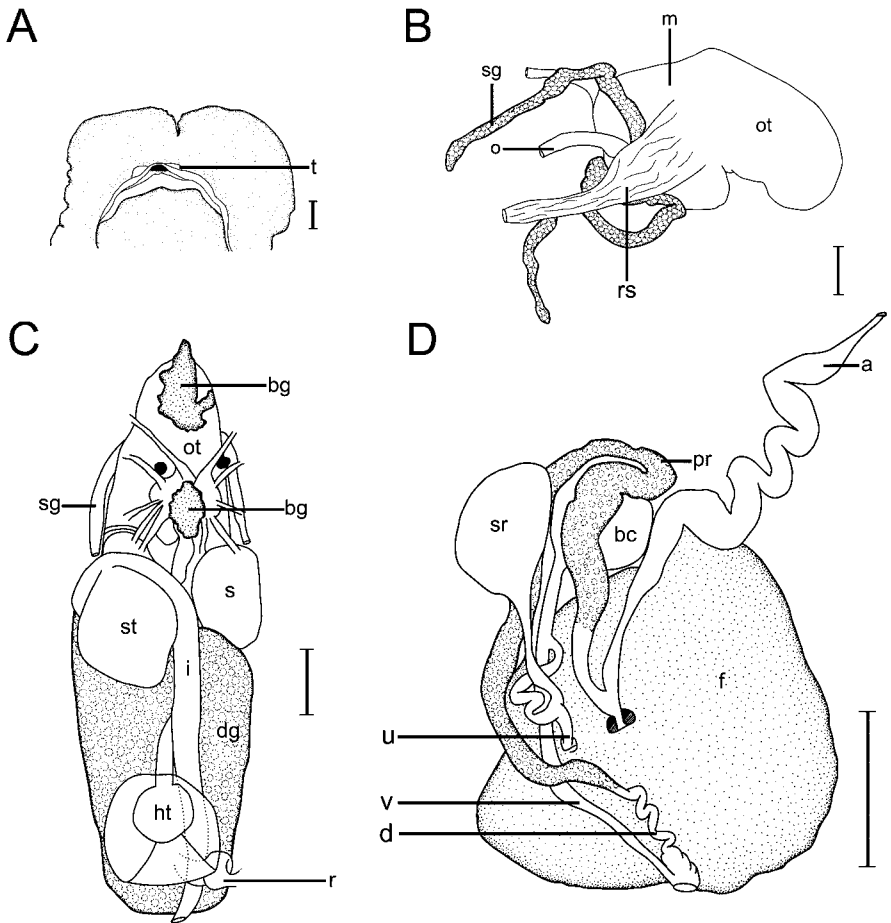


Figure 11. Anatomy of *Doris tanya* (MZUCR-INB0003118083). (A) Ventral view of the mouth area, scale bar = 1 mm. (B) Buccal bulb, scale bar = 1 mm. (C) Dorsal view of the internal organs scale bar = 1 mm. (D) Reproductive system, scale bar = 1 mm. Abbreviations: a, ampulla; bc, bursa copulatrix; bg, blood gland; d, deferent duct; dg, digestive gland; f, female gland; ht, heart; i, intestine; m, muscle; o, oesophagus; ot, oral tube; pr, prostate; r, syringe; sr, seminal receptacle; st, stomach; t, tentacle; u, uterine duct; v, vagina.

species should remain included within the genus *Doris*, which is characterized by a dorsum covered with tubercles and spicules that do not protrude from the dorsal surface, a head with two lateral tentacular prolongations, a grooved but not notched anterior border of the foot, an unarmed penis, and the absence of a vestibular gland (Valdés, 2002). The following characters exclude the species *D. tanya* as a member of the genus *Sclerodoris*: the absence of digitiform oral tentacles, the lack of caryophyllidia on the dorsum, and the presence of a grooved but unnotched foot. In addition, *Sclerodoris* is characterized by a penis armed with hooks and a lobate accessory gland without a spine (Valdés and Gosliner, 2001), features that are not present in *D. tanya*.

The specimens found in Costa Rica fit with the description provided by Marcus (1971) for *D. tanya*. However, there are two notable differences. The deferent duct

is much longer in Marcus' specimens. The duct to the seminal receptacle exists the vagina half way along its length. In Marcus's specimens (fig. 8, p. 361) the duct exits at the base of the bursa copulatrix. An intermediate condition was found in the specimens from Baja. In the specimen CASIZ071502, the deferent duct is longer than those of the specimens from Costa Rica but the seminal receptacle also exists the vagina half way along its length.

*Doris tanya* differs from other congeners found in the eastern Pacific such as *D. immonda*, *D. granulosa*, and *D. pickensi* by the external morphology and anatomy. *Doris tanya* has a notable pattern of ridges and depressions that extend longitudinally down the dorsum between the rhinophores and the gills. This pattern is composed of homogeneously distributed tubercles of different sizes. None of the other *Doris* species in the eastern Pacific have these features.

*Doris prea*, a species found in Florida and the Caribbean, is externally and internally very similar to *D. tanya*. The former species was originally described by Marcus and Marcus (1967) as a member of the genus *Anisodoris*. According to Valdés and Gosliner, 2001, *Anisodoris* is a synonym of *Diaulula*. However, *A. prea* lacks digitiform oral tentacles and caryophyllidia and therefore cannot be placed in *Diaulula*. Later, Thompson (1980) transferred *Anisodoris prea* to *Atagema*. *Atagema prea* (Marcus and Marcus, 1967) is characterized by a dorsum with tubercles but no caryophyllidia, a mid-dorsal longitudinal depression with black patches lacking tubercles, a cream-brown background, an anterior border of the foot grooved but not notched, six to eight tripinnate branchial leaves, flat oral tentacles, an unarmed penis, and the lack of an accessory gland.

Valdés et al. (2006) referred to this species as *Sclerodoris prea* (Marcus and Marcus, 1967) (p. 186). According to Valdés and Gosliner (2001), some of the main features that distinguish *Sclerodoris* from other members of the family Discodorididae are the presence of caryophyllidia, a penis armed with hooks, and a lobate accessory gland without a spine. None of these features is mentioned in the original description of *D. prea*. In addition, the description by Marcus and Marcus (1967) also states that "the tentacles are flat, broader than long, contracted," which strongly suggests that this species may be a member of the family Dorididae and likely in the genus *Doris*. Dayrat (In press) studied the phylogenetic relationships of *A. prea* and concluded that this species does not belong to Discodorididae.

When comparing the descriptions of *D. prea* by Marcus and Marcus (1967) and Thompson (1980) to the original description of *D. tanya* by Marcus, 1971 and the new data collected in our study, we concluded (based on the similarity of the external and internal features) that they are likely sister species and are both members of the genus *Doris*. *Doris prea* and *D. tanya* are similar in the following characteristics: a dorsum with composed tubercles (but no caryophyllidia) in two longitudinal rows that extend from the rhinophores to the gills, a cream-brown background with dark patches and opaque white spots, dark spots on the sole of the foot and hyponotum, tubercles around the rhinophoral and branchial sheaths, an anterior border of the foot grooved but not notched, six to eight tripinnate branchial leaves, flat oral tentacles, an unarmed penis, and the lack of an accessory gland. However, whether or not these two species are the same species remains uncertain. Further anatomical studies of newly collected *D. prea* specimens from the Atlantic should be conducted to clarify the identity of these two species.



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